INHERITANCE OF ALUMINUM TOLERANCE IN WINTER WHEAT GENOTYPES ADAPTED TO THE GREAT PLAINS REGION

by

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LITERATURE REVIEW

Soil acidity is a limiting factor for plant growth in many regions of the world (McLean, 1976; Kamprath, 1978; Adams, 1978, 1981; Clark, 1982; Foy, 1984). It has been estimated that 1455 million hectares (47 percent) of the total arable land in the world not requiring irrigation is acidic (Van Wambeke, 1976). Plants grown in acidic soils commonly display deficiencies of nitrogen, phosphorus, potassium, calcium, magnesium, and other essential elements, as well as expressing other deleterious effects due to high levels of soluble aluminum. Soils are naturally acidic either because their parent material was initially low in basic cations including Ca^{2+}, Mg^{2+}, K^{+}, and Na^{+}, or because these elements have been removed through rainfall leaching or harvest of crops (Kamprath and Foy, 1972). The natural decomposition of soils through weathering processes also increases the fraction of soluble acid cations in the soil. Cultural practices have intensified the problem of soil acidity. The long term use of acid-forming nitrogenous fertilizers causes soils to become more acidic (Pierre, 1928).

I. ACID SOILS

The phenomenon of soil acidity was discovered during the mid-nineteenth century when scientists observed that some soils turned blue litmus paper red. Later, Veitch

(1904) explained that this acidity was caused by iron, aluminum, and manganese compounds found in the soil. Not long after this, the study of soil acidity entered the modern era with the development of a technique by Sorensen (1909) to measure hydrogen-ion concentration in aqueous solution -- commonly known as a pH measurement.

After much discussion and disagreement among researchers on what exactly caused a soil to be acidic, Chernov (1947) published a book introducing the aluminum-clay theory which stated that aluminum-clays could produce base titration curves similar to those of weak acids. This theory of aluminum-clay complexes being responsible for soil acidity was not accepted until Harwood and Coleman (1954) showed that dilute acid leaching of clays produced hydrogen-clay and aluminum-clay complexes. Titration curves of the hydrogen complexes were similar to strong acids, while curves of aluminum complexes resembled weak acids.

Nevertheless, a question regarding the source of this aluminum developed. Rich and Obenshain (1955) demonstrated that much of the aluminum in soil is present as solid phase hydroxy-aluminum polymers of variable sizes and charges. Under processes of weathering or other natural decomposition, aluminum from the clay-lattice interlayer of clay minerals is released.

Soil acidity is largely determined by the soil

composition, the ion exchange, and hydrolysis reactions associated with those soil components (Thomas and Hardgrove, 1984). A common category known as titratable or total acidity has been used as one of numerous approaches to classify the components of soil acidity (Bohn et al., 1985).

Soils also can become acidic due to cultural practices. Long term use of ammoniacal fertilizer has been shown to cause a decline in soil pH (Unruh and Whitney, 1986; Mahler, 1985; Slavich 1984). Pierre (1928) studied acid-forming nitrogen fertilizers and showed that oxidation of ammonium-based fertilizers produce hydrogen ions. This situation is intensified when plant uptake of anions is greater than cation uptake (Unruh, 1989).

II. ALUMINUM TOXICITY

Poor plant growth factors -- whether one or many -- depend upon the environment, the soil type, and the plant species grown in an acidic soil. Acid soil injury has been incorrectly identified as drought injury, plant nutrient deficiency, low temperature injury, plant disease, or herbicide injury (Foy, 1974).

Decreased yields due to acid soils / aluminum toxicity have been documented. Unruh and Whitney (1986) showed that liming to increase pH on acid soils produced increased yields in 10 common hard red winter wheat (*Triticum aestivum* L.) cultivars. In a related liming study on acid soils,

Unruh reported that lower grain yield on plots with zero lime treatment was due to decreased tillering and plant population -- consequences of aluminum presence (Ph.D. dissertation, 1989). Briggs et al., (1989) in a study of early maturing Canadian cultivars, indicated an apparent relationship between high yield potential and aluminum tolerance. They suggested that this association might be related to nitrogen-use efficiency.

Foy et al., (1974b) compared yield data of wheat grown in Ohio soils which contain high levels of exchangeable aluminum. Cultivars developed in Indiana performed poorly compared to Ohio-developed cultivars.

Aluminum is a component of all soil minerals and is found in the forms of layered silicates, oxide minerals, and soluble acids (Thomas and Hardgrove, 1984). As soil becomes more acidic, either as a result of natural or man-made processes, aluminum solubilizes into the soil solution (Pierre et al., 1932). When aluminum is in solution, it is available to be taken up by root absorption. Once inside the plant tissue, detrimental effects can occur.

The exact species of aluminum (momomeric aluminum trivalent ion, Al^{+3}, or polymeric aluminum-hydroxy ion, $AlOH_x$) that produce toxic effects are not known. This is partly due to an incomplete understanding of the relationship between aluminum specie and pH. The pH value

at which aluminum becomes soluble in the soil is not well defined due to the complexity of both soil and aluminum chemistry in solution (Haug, 1984). The critical soil pH at which aluminum becomes soluble in toxic concentrations is dependent upon many soil factors including predominant clay minerals, organic matter levels, and concentration of other cations (Kamprath and Foy, 1972; Foy, 1974).

Marion et al. (1976) suggested that Al^{+3} was the toxic specie as it accounted for 100 percent of the total aluminum in solutions of pH 4.0 to pH 4.7 soils. In soybeans, Blamey et al. (1983) concluded that monomer aluminum ions were more harmful than polymer aluminum ions. The work of Tanaka et al. (1987) showed Al^{+3} to be most toxic, $Al(OH)_2$ as somewhat toxic, and $Al_2(SO_4)_3$ not very toxic to barley.

Wagatsuma and Kaneko (1987) in working with eight plant species (adzuki bean, maize, pea, peanut, oats, soybean, rice, and wheat), reported conflicting findings with those of Tanaka. They found that polymer aluminum ions were more toxic than monomer aluminum ions, and that monomer aluminum ions were more toxic than aluminum sulfate species.

III. PHYSIOLOGICAL AND BIOCHEMICAL REACTIONS

Aluminum ions directly absorbed by plant roots may be transported upward causing plant stunting and chlorosis. Ohki (1985), however, found that the majority of aluminum remains in the roots due to its low mobility. McLean and

Gilbert (1927) went further stating that aluminum was localized in the cortex of root tissue. At a cellular level, it accumulates in the protoplasm and nucleus of living cells. Working with maize, Rasmussen (1968) reported that uninjured roots effectively avoid absorbing aluminum, but as soon as lateral roots force their way through both the endodermis and exodermis, aluminum can penetrate to interior root tissue. The author postulated that when aluminum comes in contact with meristematic cells, they are damaged or "killed" and root elongation decreases or stops altogether. Electron microscope investigations by Hecht-Buchholz and Foy (1981) revealed the immediate disorganization of the plasmalemma followed by rapid breakdown of aluminum affected cells.

Another aluminum-induced biochemical change is the interference of aluminum ions with plant enzyme systems. It has been shown that aluminum ions interfere with calmodulin-stimulated ATPase activity. This interference results in severe imbalances of such cellular processes as maintenance of membrane potential, cell growth, root elongation, and chloroplast function (Siegel and Haug, 1983).

Interference in DNA replication induced by aluminum occurs when polymers become cross linked. Aluminum ions bind to the phosphorus in DNA forming a strong complex which increases the rigidity of the DNA double helix. This

results in inhibition of DNA synthesis (Matsumoto et al., 1979; Clarkson and Sanderson, 1969; Foy, 1974, 1984). Naidoo (1977) found similar results working with snap bean. He suggested that aluminum is bound to esteric phosphorus in nucleic acid and membrane lipids which brings about interference with nucleic acid replication and inhibits cell division. Working with barley, McLean (1980) found an abnormal distribution of ribosomes on the endoplasmic reticulum and postulated that aluminum interferes with protein synthesis.

Interactions between aluminum and phosphorus nutrition are evident, but difficult to discern. Phosphorus concentrations in rice tops will decrease with increasing soil aluminum concentration (Santana and Braga, 1977). Helyar (1978) showed that aluminum interference with phosphorus metabolism and pectin formation in root cell walls stopped root elongation.

Clarkson and Sanderson (1969) concluded that aluminum acts directly or indirectly to prevent the utilization of ATP in glucose phosphorylation. In general, aluminum binds phosphorus on root surfaces and cell walls in the free space of plant roots making phosphorus less available to metabolic sites within the cells. Alam et al. (1980) found that aluminum-induced iron deficiency in oats and suggested the interference of Fe^{3+} conversion to Fe^{2+} within the plant.

Calcium deficiency induced by aluminum resulting in yield reductions in alfalfa was shown by Simpson et al. (1977).

In general, excess aluminum has been reported to interfere with cell division in the root tips and lateral roots, increase cell wall rigidity by cross linking pectins, reduce DNA replication, inhibit uptake of phosphorus, interfere with enzymes involved in sugar phosphorylation and cell wall polysaccharide formation, and interfere with the uptake, transport and use of water and several essential mineral nutrients.

Isolating the exact physiological mechanisms of aluminum has been hindered by the unavailability of a suitable radioactive isotope of aluminum. The above results are common characteristics observed in plants whose root membrane structure has been changed by aluminum. These changes include short, thickened, discolored roots lacking in fine capillary branching (Fleming and Foy, 1968). Plants encountering biochemical and physiological reactions with aluminum exhibit severe stress, generally referred to as "aluminum toxicity" response.

Researchers have tried to establish a critical level of aluminum saturation to predict aluminum toxicity in soils. This is commonly measured by aluminum saturation of the cation exchange capacity. Adams (1984) concluded that critical aluminum saturation may exist, but is extremely

variable due to changes in soil types, plant species, and measurement procedures.

IV. SPECIES/GENOTYPE RESPONSE

Plant species and cultivar genotypes differ in their responses to acid soils (Neenan, 1960; Foy, 1976; Reid, 1976; Mugwira et al., 1981). In a review by Bear (1953), species grown in acid soils -- originally reported by Hartwell and Danon in 1914 -- are listed in accordance with their response. Those species which showed deleterious responses were termed sensitive and those which showed no measurable response were classified as tolerant. Species which rated very sensitive included alfalfa, lettuce, and onion. Sensitive crops included barley, red clover, sweet clover, and wheat. Species which showed a tolerant response were buckwheat, corn, cotton, and crimson clover. A very tolerant response was evident in blueberry, lupine, fescue, millet, oats, soybeans, peanut, red top, and rye.

In a review of British literature Russel (1973) concluded that barley was very sensitive to acid soils, red clover, wheat, and vetch were medium sensitive, and oats and rye were tolerant. He added that crops originating in sub-tropical regions (millet, sorghum, soybeans, and sudan grass) appear to show greater levels of tolerance to acid soils.

Response classification of plant species grown in

nutrient solution also has been documented. McLean and Gilbert (1927), and Ligon and Pierre (1932) determined barley, lettuce, beets, and timothy to be sensitive, sorghum, radishes, cabbage, oats, and rye to be medium sensitive, while corn, turnips, and redtop were tolerant to aluminum poisoning in solution culture.

Cultivars within a species also display different levels of aluminum response. Foy et al. (1965) evaluated wheat and barley varieties in acid soils and found that those wheat varieties appearing least sensitive to acid soils were developed in Brazil, Ohio, North Carolina, and Georgia -- regions where acid soils are common. Wheat varieties showing the greatest sensitivity originated in the plains and western states where acid soils are less common and aluminum toxicity is not expected. Similar results were found with barley. Foy added that certain varieties of wheat in the United States and Brazil, as well as barley in the United States, have been selected for properties that are closely associated with their abilities to tolerate aluminum in acid soils. He suggests that differences in aluminum tolerance between varieties of the same plant species could allow for increasing aluminum tolerance of commercial varieties through plant breeding.

In a study relating region of origin to levels of aluminum tolerance found in wheat, Foy et al. (1974) found

that in acid soils of Ohio, cultivars developed in Indiana performed poorly compared to those developed in Ohio. The authors suggest that Ohio cultivars have possibly been indirectly selected for greater aluminum tolerance compared to those from Indiana. In Canadian yield test of wheat cultivars derived from Brazil, Argentina, and Mexico, Mesdag and Slootmaker (1969) reported that those developed in Brazil had the highest levels of tolerance.

V. TOLERANCE MECHANISMS

The existence of a tolerance reaction is a subject of much debate among researchers. Some propose that the ability of a species or genotype to tolerate aluminum toxicity is a mechanism of avoidance or exclusion rather than an actual tolerance reaction. Although the exact mechanisms have not been isolated, possible mechanisms have been reported.

Aniol (1985) reported that aluminum tolerance varies measurably both between and within cereal species due to the rate of DNA replication and protein synthesis.

The manipulation of pH by certain genotypes has been reported by Foy et al. (1978). Tolerant plants increase the pH in the root zone thereby decreasing the solubility and toxicity of aluminum by precipitation. Another explanation of tolerance could be the differential concentrations of aluminum found in the tops and roots of plants. Also, some

plants tend to accumulate aluminum less readily than others (Foy, 1984).

Nitrification of ammonium (NH_4^+) is often inhibited in strongly acidic subsoils. Plants which can tolerate high levels of toxic NH_4^+ are usually tolerant to aluminum, suggesting an association between nitrogen metabolism and aluminum tolerance. A correlation between high kernel protein content in wheat and tolerance to acid soil was found by Mesdag et al. (1970). They concluded that the two characteristics are genetically different, but are linked to a certain extent.

In many plants, aluminum tolerance appears to be closely related to efficiency of phosphorus use. In Brazil, where aluminum toxicity and phosphorus deficiency often occur together, the ability of wheat and bean cultivars to tolerate aluminum coincides with a lower phosphorus requirement (Salinas and Sanchez, 1976). Working with soybeans differing in response to aluminum, Hanson and Kamprath (1979) showed that under high concentrations of aluminum, levels of pyruvate and ATP significantly increased in tolerant lines, while ATP levels in sensitive lines did not change. Increased uptake of potassium, magnesium, and silicon also have been shown to reduce toxic effects of aluminum.

Naturally occurring organic acids which chelate

aluminum in the plant ameliorate toxic effects (Jones, 1961). Roots of tolerant pea, maize, and barley varieties contained significantly higher concentrations of citric acid than roots of sensitive varieties (Klimashevskii and Chernsheva, 1980). Plant membranes also have shown differential response to aluminum. Dayton barley plasmalemma resisted aluminum-induced autolysis two to four days longer than Kearny barley (Hecht-Buchholz and Foy, 1981).

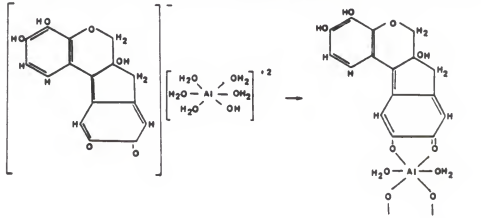
VI. SCREENING PROCEDURES

Screening procedures to determine genetic tolerance must be quick, reliable, and capable of handling large numbers of plants (Foy, 1976). Current available methods differ, but all involve exposing actively growing plants to aluminum.

Aluminum insult may be initiated by either one or a combination of two basic screening methods -- acid soil or nutrient solution. Acid soil assays involve growing plants in two aluminum concentrations and calculating an aluminum tolerance index based on yield under high and low aluminum levels (Howeler, 1987). Nutrient solution screening involves exposing plants to a range of aluminum concentrations (Foy, 1976) and directly measuring the roots. Nutrient solution techniques are considerably more precise than acid soil methods. In acidic soils, aluminum toxicity

is not the only limiting factor affecting plant growth so it is difficult to isolate aluminum response. With the nutrient solution, however, other factors can be controlled and growth response will be linked only to the effects of aluminum (Moore et al., 1976).

Polle et al. (1978) developed a nutrient solution screening technique which uses a biological stain, hematoxylin. Hematoxylin is a natural dye extracted from logwood (Hematoxylin campechianum L.). It was introduced to biological microtechnique in 1863 by German scientists. The dye solution has little or no affinity for tissue unless iron or aluminum is present. But when oxidized hematoxylin becomes negatively charged (hematin) it will mordant (chemically attach) to positively charged metallic ions and introduce color in the tissue. This useful staining technique is important in cytological research (Johansen, 1940; Gill et al., 1974). Baker (1960) proposed a hypothesized formation of the Dye/Mordant(aluminum)/tissue complex:



HEMATIN + HYDRATED ALUMINUM ION DYE COMPLEX

Polle's non-destructive hematoxylin method permits rapid visual detection of aluminum tolerance in wheat seedlings. The hematoxylin method consistently produces a recognizable zone (distinct degree of staining) dependent upon cultivar and aluminum concentration. Those cultivars which are more sensitive stain darker (i.e. accumulate more aluminum to form a darker dye complex) than more tolerant cultivars. Erichrome cyanine-r has also been used as an indicator of aluminum in plant material (Jones and Thurman, 1957).

In a study to correlate aluminum response of plants growing on acid soils and nutrient culture, Unruh (Ph.D. dissertation, 1989) found that a modification of Polle's hematoxylin staining procedure correlated extremely well with field results in separating wheat cultivars according to aluminum tolerance.

Campbell and Lafever (1976) found that cultivars rated as tolerant in the field generally had longer roots in nutrient solution. The lack of soil uniformity and interactions involved in changing soil conditions however, make soil selection by itself less than ideal. They concluded that aluminum tolerance can best be screened for in the laboratory, and confirmed by field observations of selected lines.

This procedure of combining field and laboratory

screening has proven successful at the International Maize and Wheat Improvement Center (CIMMYT) in Mexico. CIMMYT and Brazilian wheat scientists have designed a multi-location shuttle breeding program in which experimental lines are cooperatively tested at various sites in Mexico and Brazil. This shuttle program combines the yield and broad adaptation potential of CIMMYT varieties with high levels of aluminum tolerance found in Brazilian wheats. Initial identification of tolerance in experimental lines is made in the laboratory by visual scoring of the roots using a hematoxylin staining technique. Subsequent field testing at three acidic soil locations in Brazil of those lines determined to be tolerant in nutrient solution confirms tolerance (Borlaug, 1968; Rajaram et al., 1981; Rajaram et al., 1983).

VII. GENETIC IMPROVEMENT

Once differences between genotypes have been observed, the breeding and selection of plants to genetically improve tolerance to aluminum can be accomplished. The earliest attempts to breed for aluminum tolerance date back to 1919 in Brazil (da Silva, 1976).

Pavia (1944) developed a system to classify tolerance by "crestamento" -- meaning the plants had been partially burned. He suggested the association of soluble aluminum and pH was a major factor in the condition of "crestamento." In crosses between tolerant and sensitive cultivars, he

concluded that tolerance was dominant, but that the inheritance was complex.

Discontinuous variation was observed by Kerridge and Kronstad (1968) in a cross between moderately tolerant (Druchamp) and sensitive (Brevor) wheat cultivars. The authors suggested that a single dominant gene was responsible for aluminum tolerance after the F_2 generation segregated three tolerant plants to one sensitive plant.

In studying the relationship between cultivar origin and level of aluminum tolerance in wheat, Foy et al. (1974) found that the continuous range of tolerance is strong evidence that aluminum tolerance in wheat is not simply inherited. They found that considerable natural selection had occurred in areas with strongly acidic soils.

In a cross between a tolerant (IAS 54-21) and a sensitive (Crespo) cultivar, Iorczeski and Ohm (1977) found aluminum tolerance to be partially dominant -- controlled by one gene with several modifiers. Two tolerant cultivars (IAS 58, Norteno 67) appear to differ by several genes for aluminum tolerance.

Lafever et al. (1978) determined from F_1, F_2, and backcross data of tolerant/sensitive crosses between two tolerant parents (Seneca and Thorne) and two sensitive parents (Redcoat and Arthur), that sensitive lines appear to be homozygous-recessive for a single gene. They also

concluded that selection for sensitive F_2 plants was more effective than selecting for intermediate or tolerant plants, indicating that the inheritance of tolerance possessed by a line carrying a dominant allele(s) may be under complex genetic control. The authors suggested that this would explain the occurrence of sensitive lines and the absence of tolerant lines within breeding populations.

In a similar study by Campbell et al. (1978) using Atlas 66 (tolerant) and Gaines (sensitive) in addition to Seneca, Thorne, Redcoat, and Arthur, they found that dominance plays a major role in the inheritance of aluminum tolerance, and that a single gene was responsible for much of the observed dominance effect. The authors suggested that minor genes may exist and could be responsible for the significant additive effects observed in all sensitive/tolerant crosses, but that the relatively high variances of the tolerant genotypes complicated the detection of these minor genes. There was no conclusive indication of transgressive segregation in any of the crosses.

Camargo (1981) screened the progeny of tolerant (Atlas 66 and BH-1146) and sensitive (Tordo and Siete Cerros) cultivars. His results suggest that the tolerance of Atlas 66 is determined by two dominant genes. Berzonsky (1988 unpublished) obtained identical results examining the

progeny of Atlas 66 (tolerant) and Wichita (sensitive).

In crosses involving the aluminum tolerant, high-protein cultivar Atlas 66, Mesdag et al. (1970) attributed low correlation coefficients to genetic differences between the two traits, stating that only parts of the two complexes are genetically linked. They hypothesized that it is possible to screen lines for tolerance to high soil acidity in order to select within segregating populations for high kernel protein content, as long as positive selection is applied and that one of the parents combines both characteristics.

To better understand the high levels of tolerance displayed by different cultivars, Campbell and Lafever (1981) looked at the root lengths of two parents (Atlas 66 and Seneca) which displayed the highest level of tolerance among sixteen cultivars and their progeny in crosses among the remaining cultivars. All F_1 populations involving Atlas 66 as a parent were aluminum tolerant at the upper- and lower-end levels of aluminum concentration. At lower level aluminum concentrations, all F_1's involving Seneca appeared tolerant while at the upper end, the progeny of Seneca with the two most sensitive cultivars (McNair 4823 and Abe) showed reduced root lengths indicating a sensitive response. From these findings, the authors suggested that Atlas 66 possesses additional genes for tolerance not found in

Seneca.

Attempts to locate the chromosome position of the various tolerant genes have been made. Slootmaker (1974) indicates that genes involved in aluminum tolerance are located in the A and D genomes of hexaploid wheat. Prestes et al. (1975) tested the chromosome group 5 substitution lines of Atlas 66 into Chinese Spring as well as the cultivars Atlas 66 and Chinese Spring. The results indicate that chromosome 5D of Atlas 66 carries a gene or genes for aluminum tolerance and that modifying factor(s) may be present. Substituting chromosome 4D of Thatcher into Chinese Spring reduced the level of aluminum tolerance of Chinese Spring to that of Thatcher, indicating that the tolerance of Chinese Spring is located on chromosome 4D (Polle et al., 1978). To determine the location of genetic factors of aluminum tolerance in Chinese Spring, Takagi et al. (1983) evaluated a ditelosomic series and nulli-tetrasomic series of Chinese Spring. Results show that the long arms of 2D and 4D contained major genes for aluminum tolerance; minor genes were located in the long arm of 2B. Aniol and Gustafson (1984) found additional genes analyzing ditelosomic and nullisomic-tetrasomic lines of Chinese Spring. The authors suggest that these genes for aluminum tolerance are located in the short arm of 7A and 4B, and in the long arms of 6A, 2D, 3D, 4D, and 7D.

VIII. SUMMARY

Most research on the heritability of aluminum response has involved species and cultivars adapted to those regions where naturally occurring acid soils are prevalent. In areas where cultural practices are causing soil pH to decline, more knowledge about the response of regionally adapted genotypes is needed. More specifically, an inventory of genes promoting a tolerant response and the manner in which those tolerant genes are inherited is needed. Once this knowledge is common, plant breeders will be able to incorporate greater levels of tolerance into their germplasm base. Quick and accurate screening methods also must be developed and incorporated into breeding programs so that breeders may be able to evaluate large numbers of segregating genotypes for tolerance.

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INHERITANCE OF ALUMINUM TOLERANCE IN WINTER WHEAT GENOTYPES ADAPTED TO THE GREAT PLAINS REGION

INTRODUCTION

Soil acidity is a limiting factor for plant growth in many regions of the world (McLean, 1976; Kamprath, 1978; Adams, 1978, 1981; Clark, 1982; Foy, 1984). It has been estimated that 1455 million hectares (47 percent) of the total arable land in the world not requiring irrigation is acidic (Van Wambeke, 1976).

Aluminum is a component of all soil minerals (Thomas and Hardgrove, 1984) which solubilizes into soil solution as a soil becomes more acidic (Pierre et al., 1932). Plants may take up soluble aluminum through root absorption. Once inside plant tissue, such detrimental consequences as inhibition of cell division and interference with plant nutrition may occur. Plants encountering biochemical and physiological reactions with aluminum exhibit severe stress responses commonly known as "aluminum toxicity."

Plant species and cultivar genotypes differ in response to acidic soils/aluminum toxicity (Neenan, 1960; Foy, 1976; Reid, 1976; Mugwira et al., 1981). Plant species or genotypes which are adversely affected by aluminum are termed "sensitive," while those species that withstand aluminum stress are referred to as "tolerant." The exact mechanism which controls a plant's response to aluminum has not been isolated.

Exposing actively growing plants to aluminum induces

varying responses among genotypes. Selection of those plants which express aluminum tolerance may be accomplished through various screening methods. Once differences between genotypes have been established, the breeding and selection of plants to genetically improve tolerance to aluminum can be accomplished. A determination of how tolerance mechanisms are inherited equips the plant breeder with a tool to genetically improve plant tolerance levels.

Most research on the inheritance of aluminum tolerance mechanisms has involved species and cultivars adapted to those regions where naturally occurring acidic soils are prevalent. More knowledge, however, is needed about the response of genotypes adapted to regions where soils are becoming more acidic due to such cultural practices as the application of nitrogenous fertilizers (Pierre, 1928; Unruh, 1989). One such region is the central Great Plains wheat belt. The objective of this research was to study how four hard red winter wheat genotypes express response to aluminum stress; the selected cultivars are commonly grown in the Great Plains region.

A nutrient solution / hematoxylin staining technique (Polle et al., 1978) was utilized to screen F_2 populations from crosses among four parents -- an experimental line, KS831957, and three released cultivars, Victory, Chisholm, and Hawk -- for tolerance to aluminum. An additional

objective was to evaluate the value of a nutrient solution / hematoxylin staining technique in screening large segregating populations.

MATERIALS AND METHODS

Inheritance of aluminum tolerance was studied in hard red winter wheat (Triticum aestivum L.) genotypes including one experimental line, KS831957, and three released cultivars, Victory, Chisholm, and Hawk along with F_2 progeny of all possible crosses among them (without reciprocal crosses). These four parents were selected based on their differences in response to aluminum toxicity (L. Unruh, personal communication). The F_2 populations were obtained from Dr. T. S. Cox, USDA-ARS, and were screened in a modified nutrient solution / hematoxylin stain screening procedure developed by Polle et al. (1978). The F_2 populations consisted of Chisholm X Victory, Hawk X Victory, Chisholm X Hawk, Victory X KS831957, Chisholm X KS831957, and Hawk X KS831957.

SEEDLING GERMINATION

Seeds were germinated in 100 x 15 mm disposable petri-dishes on Whatman Qualitative 4 (90 mm) filter paper. Seeds were moistened with 0.10 percent Terracoat (fungicide) solution and placed in total darkness at room temperature for 12 hours. Uniform germination was attained by placing the petri-dishes in a refrigerator (total darkness at 10 degrees centigrade) for 72 hours. The petri-dishes were then removed and placed in total darkness at room temperature for 36 hours. Seedlings were transferred to

nutrient solution after the roots had reached a length of 10 - 20 mm.

NUTRIENT SOLUTION

Nutrient solution was contained in plastic photographic developing trays (330 x 420 mm) at a volume of 2 L / tray. The nutrient solution consisted of 5 mM $CaCl_2$, 6.5 mM KNO_3, 2.5 mM $MgCl_2$, 0.1 mM $(NH_4)_2SO_4$, and 0.4 mM NH_4NO_3. The pH was adjusted to 4.00 with 0.25 N HCl (Polle et al., 1978).

Seedlings of uniform root length were supported on plastic mesh screens (170 x 350 mm) which floated on the solution surface. The screen was divided into 54 grids (40 x 40 mm) using a permanent marker. Seedlings were transplanted from the petri dish to their respective grids (two plants per grid) by threading the three primary roots through openings (2 x 2 mm) in the screen. To maintain high humidity, the seedlings were sprayed with a fine mist of distilled-deionized water immediately after transplanting. In each tray, a total of 108 seedlings were maintained at a volume of 18.5 ml nutrient solution per plant, and were exposed to continuous light and aeration for 24 hours.

ALUMINUM TREATMENT

After 24 hours, the nutrient solution was discarded and replaced with fresh nutrient solution (pH 4.00) containing the respective aluminum treatment -- 0.00 mM, 0.30 mM, 0.60 mM, and 1.20 mM aluminum -- for 17 to 20 hours. The

source of aluminum was 0.1 M aluminum stock solution (pH 3.30) made by adding 17.896 g of $AlCl_3 \cdot 6H_2O$ to one liter of nutrient solution. The number of plants per volume of treatment solution was again 18.5 ml / plant under constant light and aeration. After aluminum treatment, seedlings were washed in 1.5 L aerated distilled-deionized water for 45 minutes to remove any aluminum that was bound to the root surface.

HEMATOXYLIN STAINING

The hematoxylin stain was made by stirring 2.0 g certified hematoxylin (Sigma Chemical Co.) and 0.2 g $NaIO_3$ (oxidizing agent) in 1 L of distilled-deionized water for 10 to 12 hours using a magnetic stirrer. Seedlings were placed in the hematoxylin solution for 15 minutes at a volume of 1 L / tray (9.25 ml / plant). Seedling roots were rinsed in flowing distilled water and placed in 1.5 L aerated distilled-deionized water for one hour after treatment.

VISUAL SCORING

Each root of each seedling was given a visual score ranging from zero to four. The rating was based upon the degree of staining of the root tip. Each root was evaluated against a white background with a score of zero representing no staining of the root tip. Root tips with stain just discernible received a score of one; if the degree of stain

equaled ~ 33 percent of the root tip area while the remaining ~ 66 percent of the root tip did not stain a two was given; and a score of three was recorded if ~ 66 percent of the root tip stained while ~ 33 percent did not. A score of four was given if the entire root tip was completely stained. A mean observation for each seedling was calculated based on the individual scores of each root tip.

EXPERIMENTAL DESIGN

The design of the experiment was a randomized complete block consisting of four treatments replicated eight times, measured over time.

Each replicate consisted of four trays (1 tray / treatment). The mesh screen in each treatment was divided into six blocks, each block containing 14 F_2 seedlings, randomly drawn from the six crosses, plus one seedling of each parent, all randomized within the block.

STATISTICAL ANALYSIS

The mean observation of each seedling -- ranging from 0.00 to 4.00 (0.00 being tolerant, 4.00 being sensitive) -- was categorized according to genotype. Histograms showing the frequency of distribution at each treatment level, were constructed for each F_2 and parent. The distribution was divided into eight class intervals of width 0.50. Those observations which fell on endpoints of class intervals were rounded up to the next class (except for those mean

observations of 4.00 which remained in the last class interval).

LABORATORY EQUIPMENT AND CONDITIONS

Measurements of pH were made using a Corning pH meter model 125, with an Orion-Ross combination glass electrode. Daily calibration of the meter was made using Fisher Scientific certified buffer solutions, pH 4.00 and pH 7.00. All solutions were made with distilled-deionized water (pH 4.73) and were magnetically stirred and volumetrically measured.

Illumination (50 to 90 micro einsteins m^{-2} sec^{-1}) was produced by six fluorescent Phillips brand 40 watt Agro-lites suspended 450 mm above the seedlings. Room temperature was constantly 25 to 27 degrees centigrade, and solution aeration was provided with a Penn-Plax brand X440 aquarium pump through plastic tubing.

RESULTS

Hematoxylin staining was successful in separating both parent and F_2 populations for sensitivity/tolerance to aluminum. Sensitive seedling root tips stained darkly while tolerant seedlings showed little staining. Root tips were rated by a visual estimation of staining intensity based on a scale of 0.00 to 4.00. A tolerant response received a score of 0.00 and a sensitive response was rated 4.00.

Analysis of variance for root tip observations is reported in Table 2. Significant differences were observed for parents, F_2 populations and level of aluminum. There was no overall difference, however, in parent and F_2 means. Aluminum treatment X entry interaction was significant, therefore different parents and crosses responded differently to increasing levels of aluminum. Mean observations from the 0.30 mM, 0.60 mM and 1.20 mM levels of aluminum were used in the analysis of variance. The 0.00 mM level was not included due to a limited number of available seedlings as a result of poor germination.

Mean root tip scores are given in Table 3. Parents were specifically selected based upon their response to aluminum under hematoxylin staining techniques as reported by Unruh (1989).

Victory is considered to be sensitive to aluminum. It consistently stained sensitive at all three aluminum levels,

with mean scores of 3.77, 3.99 and 4.00 at 0.30, 0.60, and 1.20 mM aluminum, respectively.

Chisholm is considered to be intermediate in its response to aluminum. It received an intermediate rating at the 0.30 mM Al level (mean 1.93), but sensitive scores at the 0.60 mM (mean 3.68) and 1.20 mM Al (mean 3.98) levels.

Hawk and KS831957 are considered to be tolerant to aluminum. In this study, Hawk was tolerant at the 0.30 mM Al level (mean 0.77), intermediate at the 0.60 mM Al level (mean 2.84), and sensitive at the 1.20 mM Al level (mean 3.89). KS831957 was significantly more tolerant to aluminum than Hawk at all three levels with mean scores of 0.43, 1.69 and 3.30 at 0.30 mM, 0.60 mM and 1.20 mM Al, respectively.

Significant separation of the four parent cultivars can be ascertained at the 0.30 mM aluminum level (Figure 1) based on root tip staining response to aluminum. At the 0.60 mM Al treatment, both Victory and Chisholm rated sensitive and were significantly different from Hawk and KS831957. At the 1.20 mM Al treatment, all four cultivars can be considered sensitive to aluminum based upon staining observations. KS831957, however, showed significantly less stain in the root tips than the other three parent genotypes.

Mean values for the F_2 populations are reported in Table 3. Populations based upon the parental reactions can

be grouped into three categories: sensitive X sensitive, sensitive X tolerant, and tolerant X tolerant. In the Chisholm X Victory population (sensitive X sensitive), the mean response was 2.74 at an aluminum concentration of 0.30 mM. This was significantly higher than the scores for three of four sensitive X tolerant crosses -- Hawk X Victory, Chisholm X Hawk, and Victory X KS831957. The Chisholm X KS831957 (sensitive X tolerant) F_2 population, however, had a mean score of 2.73. This was nearly equal to the 2.74 mean of the Chisholm X Victory (sensitive X sensitive) cross.

At 0.30 mM aluminum concentration, the Hawk X KS831957 (resistant X resistant) F_2 population mean response (1.75) was greater (less tolerance exhibited) than the responses of the more tolerant parent genotypes, KS831957 (0.43) and Hawk (0.77).

Histograms with overall mean and range of response best display the intensity of stained root tips. Parent and F_2 population histograms are found in Figures 2 through 11.

Victory contained a majority of sensitive seedlings at the 0.30 mM aluminum level, and all sensitive seedlings at the 0.60 and 1.20 mM levels (Figure 2).

Chisholm had a median score of 2.25 at the 0.30 mM Al level (Figure 3), and has a normal distribution around that intermediate value. At the 0.60 and 1.20 mM Al levels, root

tip mean scores shifted to 3.75 - 4.00.

Hawk showed a tolerant response at the 0.30 mM Al level (Figure 4) with a majority of the seedlings being rated 1.25 or less. At the 0.60 mM Al level, Hawk stained greater than 2.25, and all the seedlings scored 3.75 - 4.00 at the 1.20 mM Al level.

A similar response was observed with KS831957 (when compared to Hawk) except that KS831957 tended to be slightly more tolerant at all three levels of aluminum (Figure 5). At the 0.60 mM Al treatment level roughly 50 percent of the seedlings rated below 2.25 for root tip staining. At the 1.20 mM Al level a majority of KS831957 seedlings scored above 3.25 in root tip staining.

Based upon the data presented in this thesis and the data previously reported by Unruh (1989), a separation of sensitive and tolerant responses was assigned at 2.25. This value classified Victory as sensitive, Chisholm as intermediate, and Hawk and KS831957 as tolerant at the 0.30 mM Al level of aluminum. The best separation of all four parents was observed at the 0.30 mM Al level; higher concentrations of aluminum forced the distributions of the four parent cultivars into one category -- sensitive. Classification of the F_2 populations is thus focused on the 0.30 mM Al level.

Reactions of the six F_2 populations are located in

Figures 6 through 11. Classification for each population is based upon separation at 2.25 (tolerant vs. sensitive) at the 0.30 mM level. For the Chisholm X Victory population, 100 of 112 F_2 seedlings (almost 90 percent) were classified sensitive (Table 4).

Previous researchers have verified that aluminum tolerance in wheat is simply inherited and controlled by dominant genes; therefore, Mendelian ratios were tested.

Two Hawk crosses (Hawk X Victory, Chisholm X Hawk) produced populations which suggest that Hawk contains one dominant gene controlling aluminum tolerance. In the Hawk X Victory cross, a chi-square value testing a ratio of 3 tolerant : 1 sensitive fit with a probability > 0.95. For the Chisholm X Hawk cross, a chi-square value for a 3:1 goodness of fit ratio with a probability > 0.95 was calculated. Both of these populations support the assumption that Hawk contains one dominant gene for aluminum tolerance.

For the crosses involving KS831957, the segregation pattern is less clear. In the Victory X KS831957 cross, a large majority of the F_2 seedlings scored in the tolerant range. This population fits neither a 15:1 ratio (two dominant genes) or a 3:1 ratio (one dominant gene) (Table 4). The excessive number of tolerant seedlings appearing in the F_2 population suggest, however, that KS831957 contains

at least one (possibly two) gene(s) affecting aluminum response. For the cross Chisholm X KS831957, the high number of sensitive segregates is unusual. If dominant genes initiate an aluminum tolerance response in the plant, progeny from this cross should contain a majority of tolerant individuals.

In the population involving the two tolerant parents, Hawk X KS831957, two large classes of tolerant and sensitive seedling are observed (Figure 11). Crosses involving tolerant genotypes that produce sensitive segregates indicate that the two parents contain different genes affecting aluminum tolerance. The large sensitive class, however, does not correspond to expected two- or three- gene Mendelian models for independent dominant genes.

DISCUSSION

Screening either fixed lines (parents) or segregating populations for tolerance to aluminum using a nutrient solution / hematoxylin staining technique provides a method to determine genotypic response to aluminum. This technique correlates well with field observations (Unruh, 1989) and allows wheat breeders to screen large segregating populations for aluminum tolerance. The International Maize and Wheat Improvement Center (CIMMYT) wheat breeding program has used this technique to screen and identify aluminum-tolerant segregates (Borlaug, 1968; Rajaram et al., 1981, 1983).

In this study, three concentrations of aluminum separated the tolerance response of four hard red winter wheats into recognizable groups. A concentration of 0.30 mM Al was most effective in separating the four wheats (Figure 1). All genotypes exhibited a range of responses, with Chisholm having the most variation. Since all of these hard wheats represent F_4 to F_7 bulks it is quite probable that they may be heterogeneous for aluminum tolerance.

A second possible explanation of the observed variation could be that the seed germinated non-uniformly, even though attempts for uniform germination were made. Those seedlings which produced a radicle but no shoot probably differed in ion uptake compared to seedlings which actively produced

roots and shoots.

Re-selection within each of the parents is being done to determine the repeatability of the hematoxylin staining technique at different levels of aluminum.

Victory is considered to be extremely sensitive to aluminum and was the most sensitive genotype by hematoxylin staining technique in this study. Chisholm placed intermediate at the low level and sensitive at the two higher levels of aluminum. Hawk and KS831957 were tolerant at the 0.30 mM level while being intermediate at the 0.06 mM level and sensitive at 1.20 mM Al level.

Inheritance to aluminum tolerance in the four hard red winter wheats studied is apparent for Victory and Hawk, but unclear for Chisholm and KS831957. It is possible that there exists one or more multiple allelic series with dominance in the order Chisholm > KS831957 > Victory. Minor or modifying genes may also help explain this ambiguity. The presence of modifying or minor genes which may produce additive tolerance has been reported by Iorczeski and Ohm (1977) and Campbell and Lafever (1978). Finally, because the exact parental plants used in the crosses were not available, the possibility of genetic variation among parents of different crosses cannot be ruled out.

Almost 90 percent of Chisholm X Victory seedlings scored in the sensitive range (Figure 6). This suggests

that Victory and Chisholm do not carry genes for tolerance. Victory is clearly sensitive to aluminum, because it has no tolerant genes present (Figure 2). Chisholm, however, does express an intermediate tolerant response at 0.30 mM Al level, so some modifying action of minor genes may be present in Chisholm (Figure 3).

The inheritance of KS831957 does not quite fit the one (3:1) or two (15:1) dominant gene ratios expected from inheritance data reported for other tolerant genotypes (Kerridge and Kronstad, 1968; Campbell and Lafever, 1978). The Victory X KS831957 F_2 population fell between a 3:1 and a 15:1 ratio, which would indicate that KS831957 contains one or two genes for aluminum tolerance. The probability for a 3:1 ratio was slightly higher (Table 4). Based on this cross, one possibility is that KS831957 contains two genes for tolerance with unequal effects and partial dominance, so that some genotypes heterozygous at a single locus fell into the sensitive range. Modifying action of minor gene(s) which produce additive tolerance may also be present in KS831957.

In tests involving the parents it was shown that KS831957 is less sensitive to aluminum than Hawk, supporting the hypothesis that KS831957 may have additional sources for tolerance. Neither Hawk nor Victory showed responses which would suggest such modifiers.

Hawk X Victory and Chisholm X Hawk F_2 populations segregated in a 3:1 tolerant to sensitive genetic ratio with a probability > 0.95. This suggests that Hawk contains one dominant gene for tolerance to aluminum.

The Chisholm X KS831957 cross had an excessively high number of sensitive F_2 segregates. If dominant genes do affect aluminum tolerance, expected segregation would favor the dominant response. Since both parents were not uniform in their response to aluminum, it is possible that the original crosses involved sensitive genotypes within KS831957 and Chisholm. This cross should be repeated using individual plants previously screened for aluminum response.

In the Hawk X KS831957 cross, a large proportion of F_2 seedlings exhibited a sensitive response, indicating that the two parents contain different genes for tolerance to aluminum. However, when the parent and F_2 seedlings are compared at the 0.60 mM Al treatment level, no F_2 segregates exceed the tolerance observed in KS831957.

In conclusion, hard winter wheats do contain genes affecting aluminum tolerance as estimated by hematoxylin staining. Screening germplasm or segregating populations at various concentrations of aluminum in nutrient solution provides a reasonable assay of how these materials may react to aluminum under acidic soil conditions. This material can be readily incorporated into conventional breeding programs.

From this study the following statements can be made about the four wheat genotypes studied.

Victory does not seem to have any aluminum tolerant genes. Chisholm appears to have components which modify aluminum tolerance at low levels of aluminum, but not a specific tolerant gene. Hawk appears to possess one dominant gene that controls aluminum response. KS831957 may contain one or two dominant genes with unequal effects, possibly with modifying genes that amplify the effect of the tolerance gene(s). Hawk and KS831957 can be used as sources of aluminum tolerance to improve this trait in future hard winter wheat varieties.

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TABLES AND FIGURES

TABLE 1. Nutrient solution used for growing seedlings (Polle et al., 1978).

COMPOUND	FORMULA	mM	F.W.
CALCIUM CHLORIDE	$CaCl_2$	5.0	110.99
POTASSIUM NITRATE	KNO_3	6.5	101.11
MAGNESIUM CHLORIDE	$MgCl_2 \cdot 6H_2O$	2.5	203.31
AMMONIUM SULFATE	$(NH_4)_2SO_4$	0.1	132.14
AMMONIUM NITRATE	NH_4NO_3	0.4	80.04

TABLE 2. Analysis of variance for root tip scores of four parents and six F_2 populations stained in hematoxylin after exposure to three levels (0.30, 0.60, and 1.20 mM) of aluminum.

SOURCE	DF	SS	MS	F	Pr>F
REPLICATION	7	110.72	15.81	140.66	0.0001
Al TREATMENT	2	1517.15	758.57	6745.56	0.0
ENTRY	9	719.46	79.94	710.86	0.0
PARENTS VS. CROSSES	1	0.15	0.15	1.37	0.2428
AMONG PARENTS	3	449.15	149.71	1942.08	0.0
AMONG CROSSES	5	270.15	54.03	445.85	0.0001
Al TREATMENT * ENTRY	18	229.43	12.74	113.35	0.0001

TABLE 3. Mean root tip scores for parents and their respective crosses at three levels of aluminum concentration.

ENTRY	TREATMENT (mM Aluminum) 0.30	0.60	1.20
PARENTS			
VICTORY	3.43	3.99	4.00
CHISHOLM	1.93	3.68	3.98
HAWK	0.77	2.84	3.89
KS831957	0.43	1.69	3.30
CROSSES			
CHISHOLM X VICTORY	2.74	3.82	3.98
HAWK X VICTORY	1.35	2.93	3.86
CHISHOLM X HAWK	1.36	2.87	3.79
VICTORY X KS831957	0.67	2.41	3.58
CHISHOLM X KS831957	2.73	3.64	3.93
HAWK X KS831957	1.75	2.18	3.77

$LSD_{0.05}$ (PARENTS VS CROSSES) = 0.308
$LSD_{0.05}$ (PARENTS) = 0.272
$LSD_{0.05}$ (CROSSES) = 0.341

TABLE 4. Chi-square probabilities of segregating F_2 populations (tolerant : sensitive) at 0.30 mM aluminum concentration.

CROSS	RATIO OBSERVED	RATIO TESTED	PROBABILITY
CHISHOLM X VICTORY	12:100	|———sensitive———|	
HAWK X VICTORY	81:26	3:1	Pr>0.975
CHISHOLM X HAWK	66:21	3:1	Pr>0.975
VICTORY X KS831957	92:16	3:1	0.10>Pr>0.05
		15:1	Pr<0.005
CHISHOLM X KS831957	21:80		
HAWK X KS831957	37:24		

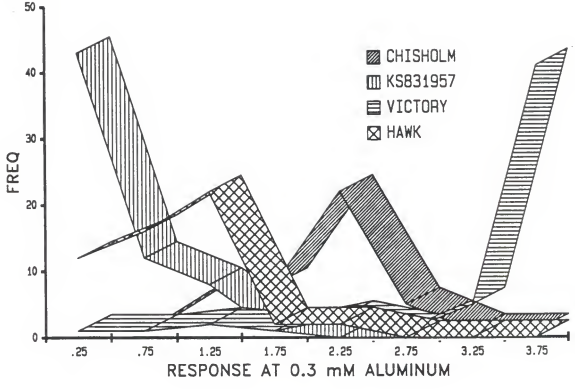


FIGURE 1. Separation of parent genotypes at 0.30 mM aluminum concentration, based on root tip staining with hematoxylin.

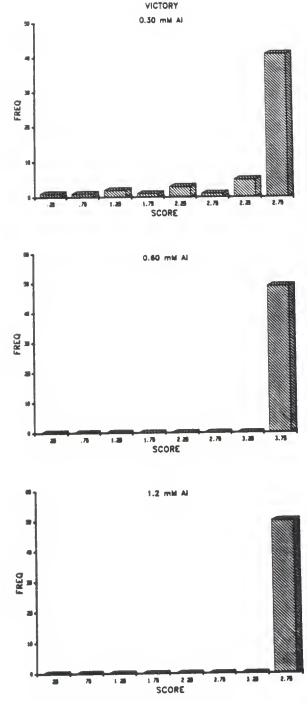


FIGURE 2. Histograms for cultivar Victory wheat seedling root response to three levels of Al in nutrient solution measured by hematoxylin staining technique (score of 0.00 to 4.00 for tolerant to sensitive).

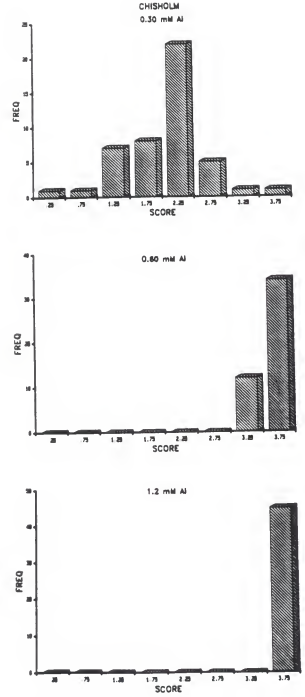


FIGURE 3. Histograms for cultivar Chisholm wheat seedling root response to three levels of Al in nutrient solution measured by hematoxylin staining technique (score of 0.00 to 4.00 for tolerant to sensitive).

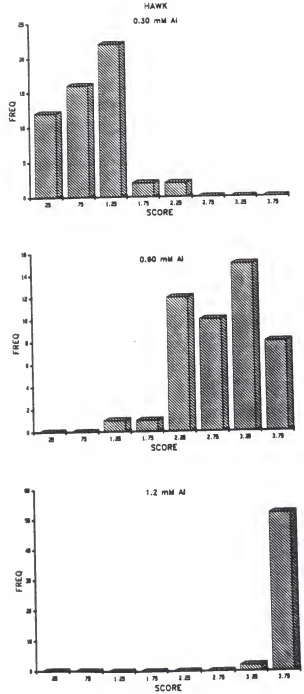


FIGURE 4. Histograms for cultivar Hawk wheat seedling root response to three levels of Al in nutrient solution measured by hematoxylin staining technique (score of 0.00 to 4.00 for tolerant to sensitive).

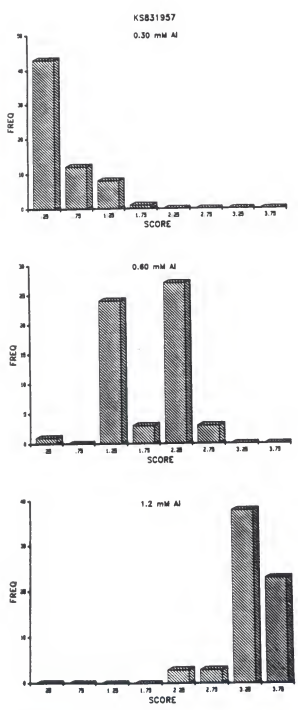


FIGURE 5. Histograms for experimental line KS831957 wheat seedling root response to three levels of Al in nutrient solution measured by hematoxylin staining technique (score of 0.00 to 4.00 for tolerant to sensitive).

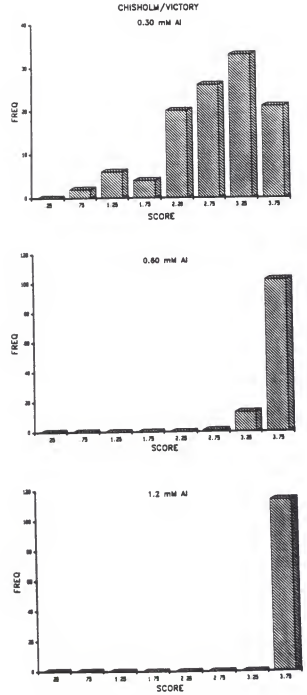


FIGURE 6. Histograms for F_2 progeny Chisholm X Victory wheat seedling root responses to three levels of Al in nutrient solution measured by hematoxylin staining technique (score of 0.00 to 4.00 for tolerant to sensitive).

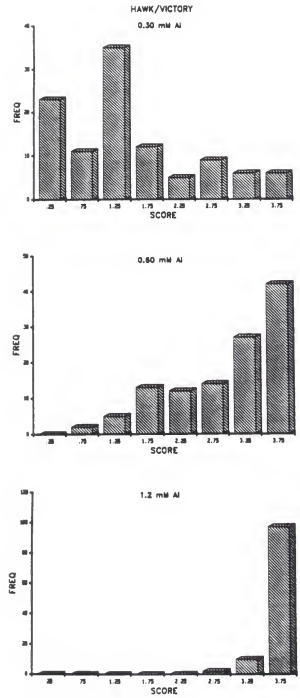


FIGURE 7. Histograms for F_2 progeny Hawk X Victory wheat seedling root response to three levels of Al in nutrient solution measured by hematoxylin staining technique (score of 0.00 to 4.00 for tolerant to sensitive).

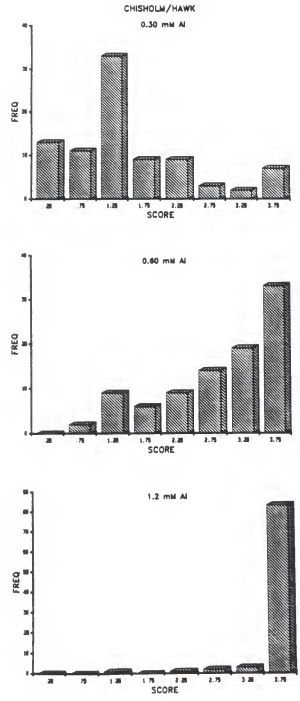


FIGURE 8. Histograms for F_2 progeny Chisholm X Hawk wheat seedling root response to three levels of Al in nutrient solution measured by hematoxylin staining technique (score of 0.00 to 4.00 for tolerant to sensitive).

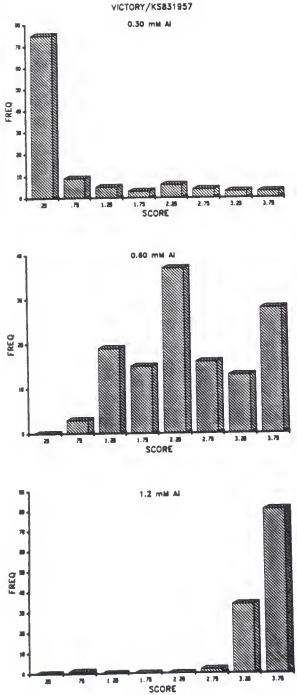


FIGURE 9. Histograms for F_2 progeny Victory X KS831957 wheat seedling root response to three levels of Al in nutrient solution measured by hematoxylin staining technique (score of 0.00 to 4.00 for tolerant to sensitive).

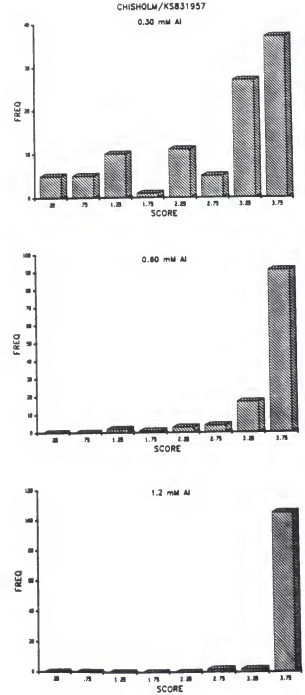


FIGURE 10. Histograms for F_2 progeny Chisholm x KS831957 wheat seedling root response to three levels of Al in nutrient solution measured by hematoxylin staining technique (score of 0.00 to 4.00 for tolerant to sensitive).

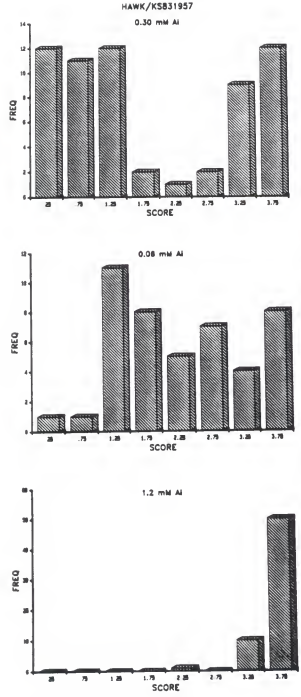
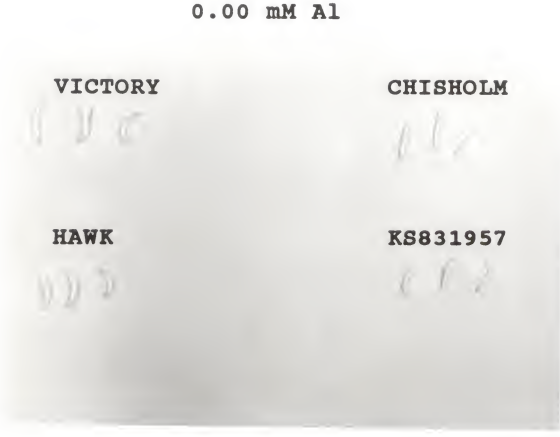
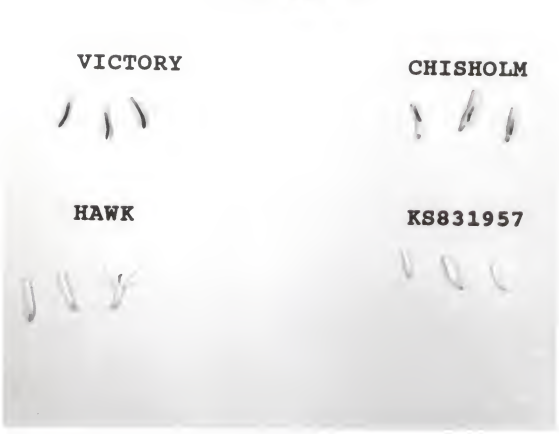


FIGURE 11. Histograms for F_2 progeny Hawk X KS831957 wheat seedling root response to three levels of Al in nutrient solution measured by hematoxylin staining technique (score of 0.00 to 4.00 for tolerant to sensitive).

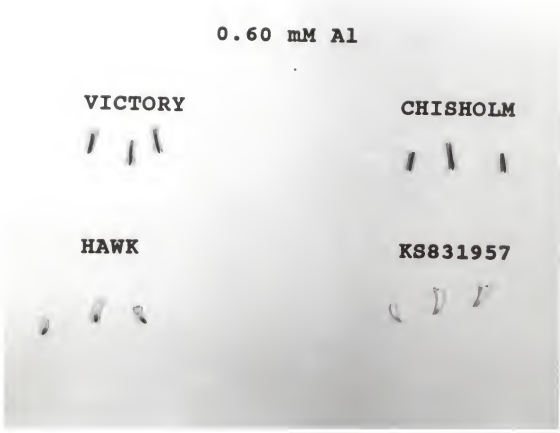
APPENDIX



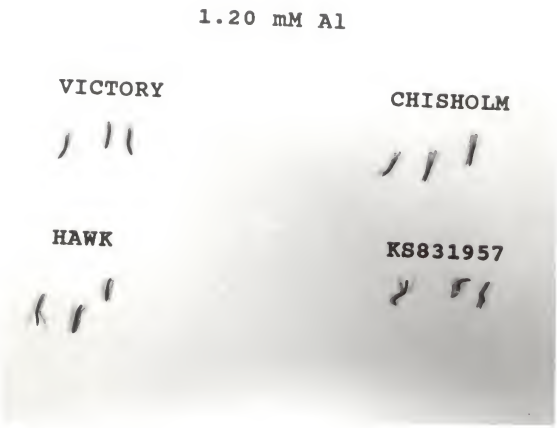
Seedling root tip staining of four hard red winter wheats with hematoxylin after 20 hours exposure to 0.00 mM aluminum.



Seedling root tip staining of four hard red winter wheats with hematoxylin after 20 hours exposure to 0.30 mM aluminum.



Seedling root tip staining of four hard red winter wheats with hematoxylin after 20 hours exposure to 0.60 mM aluminum.



Seedling root tip staining of four hard red winter wheats with hematoxylin after 20 hours exposure to 1.20 mM aluminum.

INHERITANCE OF ALUMINUM TOLERANCE IN WINTER WHEAT GENOTYPES ADAPTED TO THE GREAT PLAINS REGION

by

K. SCOTT DORSCH

B.S., Kansas State University, 1987

AN ABSTRACT OF A MASTER'S THESIS

submitted in partial fulfillment of the

requirements for the degree

MASTER OF SCIENCE

Department of Agronomy

KANSAS STATE UNIVERSITY
Manhattan, Kansas

1989

ABSTRACT

Identifying winter wheat (Triticum aestivum L.) genotypes which display a tolerant response to aluminum is important in breeding programs, especially in regions where acid soils are naturally occurring or where soils are becoming acidic as a consequence of cultural practices.

Screening fixed lines or segregating populations using a nutrient solution / hematoxylin screening procedure provides an inexpensive and accurate method to determine genotypic response to aluminum. This experiment consisted of a four parent half-diallel of hard red winter wheat including one experimental line, KS839157, and three released cultivars, Chisholm, Hawk, and Victory. Seedlings of six F_2 populations and the four parent lines were evaluated in a randomized complete block design consisting of three aluminum levels (0.30, 0.60, and 1.20 mM Al) replicated eight times. Seedling response to aluminum was estimated by visually rating each root tip on a score ranging from zero (tolerant) to four (sensitive).

Frequency distributions for each parent and F_2 population were constructed to interpret the segregation ratios. Response scores were placed in eight classes with tolerant vs. sensitive classification based on parental response.

Victory is sensitive and homogeneous in its response to

aluminum. Chisholm shows an intermediate response at 0.30 mM Al, but is sensitive at 0.60 and 1.20 mM Al. At 0.30 mM Al, Chisholm seedling scores ranged from 1.00 to 4.00 with a median of 2.25. It may have components which modify aluminum response. Hawk shows one dominant gene conferring aluminum tolerance at 0.30 mM, but is not effective at 0.60 and 1.20 mM Al. KS831957 may contain one or two dominant genes with unequal effects, possibly with modifying genes that amplify the effect of the tolerance gene(s). The source of tolerance in KS831957 is different than that found in Hawk.

Aluminum tolerance as expressed by hematoxylin root tip staining is simply inherited and dominant in tolerant Great Plains wheats. Breeding for aluminum tolerance using these methods is straightforward and effective.